Vol. 99. Part 6. Pp. 245-268, 6 figs. 25th June, 1948

COMMONWEALTH INST. ENTOMOLOGY LIBRARY
14 AUG 1948
SERIAL Ent. 344
SEPARATE

(pt. 7 rec'd 8/7/48)

E & A

THE TRANSACTIONS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

PAGES

WALOFF, N., Ph.D., NORRIS, M. J., Ph.D. (MRS. O. W. RICHARDS), and BROADHEAD, E. C., B.Sc. Fecundity and Longevity of *Ephestia elutella* Hübner (Lep., PHYCITIDAE) . . 245–268, 6 figs.

LONDON
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 7s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1948-1949

C. B. Williams, M.A., Sc.D., *President.*
G. Fox-Wilson, N.D.H.
B. M. Hobby, M.A., D.Phil. } *Vice-Presidents.*
Miss C. E. Longfield

A. Welti, *Treasurer.*

N. D. Riley, *Secretary.*

E. B. Britton, M.Sc., *Editor.*

Other Members of Council.

R. L. E. Ford.
R. M. Greenslade.
A. G. Hamilton, B.Sc., B.Agr., Ph.D., D.I.C.
Capt. R. A. Jackson, C.B.E., R.N.
H. B. D. Kettlewell, M.A., M.B., B.Chir., M.R.C.S., L.R.C.P.
A. M. Massee, D.Sc.
G. E. J. Nixon, B.A.
J. A. Simes, O.B.E.
W. H. Thorpe, M.A., Sc.D.
A. J. A. Woodcock, M.Sc.

Miss E. Evans, *Registrar.*

Finance and House Committee.

G. Fox-Wilson, N.D.H. (Chairman).

C. L. Collenette.
A. G. Gabriel.
H. E. Hinton, B.Sc., Ph.D.
Capt. R. A. Jackson, C.B.E., R.N.
A. M. Massee, D.Sc.

Publication and Library Committee.

W. H. Thorpe, M.A., Sc.D. (Chairman)

Prof. G. D. Hale Carpenter, M.B.E., D.M.
A. G. Hamilton, B.Sc., B.Agr., Ph.D., D.I.C.
G. E. J. Nixon, B.A.
J. Smart, B.Sc., Ph.D.
T. H. C. Taylor, D.Sc.

Committee on Generic Nomenclature.

Francis Hemming, C.M.G., C.B.E. (Chairman).

W. A. F. Balfour-Browne, F.R.S.E.
K. G. Blair, D.Sc.
O. W. Richards, M.A., D.Sc.
N. D. Riley (Secretary).

Committee for the Protection of British Insects.

H. M. Edelsten, O.B.E. (Chairman)

R. B. Benson, M.A.
E. A. Cockayne, M.A., M.D., F.R.C.P.
R. L. E. Ford.
B. M. Hobby, M.A., D.Phil.
Capt. R. A. Jackson, C.B.E., R.N.
Col. F. A. Labouchere.
A. M. Massee, D.Sc.
The Hon. Miriam Rothschild.
N. D. Riley (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Francis Hemming, C.M.G., C.B.E., appointed 1946.
   Dr. V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S., appointed 1943.
2. **Local Committee of Management of Wicken Fen.**
   Mr. H. M. Edelsten, O.B.E. [nominated by Committee for the Protection of British Insects].
3. **National Trust for Places of Historic Interest or Natural Beauty**
   Mr. H M. Edelsten, O.B.E., appointed 1944.
4. **New Forest Association.**
   Mr. W. Fassnidge, appointed 1934.
5. **New Forest Joint Committee.**
   Mr. W. Fassnidge, appointed 1939.
   Dr. F. J. Killington, D.Sc., A.L.S., appointed 1939.
6. **Royal Meteorological Society. Phenological Committee.**
   Dr. C. B. Williams, M.A., D.Sc., appointed 1937.
7. **Council for the Promotion of Field Studies.**
   Dr. W. H. Thorpe, M.A., Sc.D., appointed 1944.
8. **Joint Bioclimatic Committee.**
   Dr. B. P. Uvarov, C.M.G., D.Sc., appointed 1945.
   Dr. C. B. Williams, M.A., D.Sc., appointed 1945.
9. **Yorkshire Naturalists' Trust, Ltd.**
   Mr. W. D. Hincks, M.P.S., appointed 1946.

FECUNDITY AND LONGEVITY OF *EPHESTIA ELUTELLA* HÜBNER (LEP. PHYCITIDAE)

By Miss N. Waloff, Ph.D., Maud J. Norris, Ph.D. (Mrs. O. W. Richards), and Mrs. E. C. Broadhead, B.Sc.[1]

Manuscript received 2nd July, 1947.
(Read 19th November, 1947.)

With 6 Text-figures.

Initially, the aim of this work was to provide the data necessary for the numerical estimations in the population study of this species, made in a London granary (Richards and Waloff, 1946).

The contents of this paper are divided into the following sections :—

PAGE

A. Methods 245

B. Longevity and fecundity of the wild stock reared on Manitoba Wheat 246

(i) Relation between the weights of the moths on emergence and fecundity and longevity 247

(ii) The effect of temperature on fecundity and longevity of the moths 251

(iii) Effect of drinking water on fecundity and longevity ... 256

(iv) Longevity of virgin females and resorption of egg rudiments 256

C. The effect of diapause and utilisation of the stored food on the fecundity of the moths 257

D. The effect of larval food on the fecundity of the adults 259

(i) Preliminary experiments with a non-diapausing stock of larvae 259

(ii) Experiments with the diapausing stock of larvae ... 260

E. Oviposition 263

F. Discussion 264

G. Acknowledgments 266

H. Summary 266

References 267

A. Methods.

The moths in these experiments were obtained from different sources. Most of them were from the warehouse, and others were from the laboratory stock.

[1] This author was a member of the Staff of the Pest Infestation Laboratory, D.S.I.R.

(*a*) In the laboratory experiments the fully grown larvae were allowed to crawl into the small tubes formed by rolling up strips of corrugated paper. There they pupated. The individuals were separated by unrolling and cutting up the paper, and each was placed in a glass tube. This avoided the actual handling of the pupae. On emergence the imagos were sexed, weighed (in the later experiments) and set up in pairs in 3-inch by 1-inch glass tubes fitted with muslin topped bored corks. In the initial experiments the males were removed after twenty-four hours, but in all the later ones they were removed immediately after pairing. Each tube was numbered, and the female provided with a piece of black paper on which to oviposit. In some experiments water to drink was given by inserting a piece of moistened filter paper 3 cm. by 1 cm. long, which adhered to the side of the tube. The tubes were kept in an unheated outhouse, or in a black box in a controlled temperature room at 25° C. and 70 per cent. relative humidity. To prevent damage to the eggs, the female was removed daily to a clean tube. The eggs were counted every twenty-four hours and a record was kept of the incubation period and the numbers of larvae hatching.

Throughout this work the term fecundity is taken to mean the number of eggs laid by a female. The "potential" fecundity means the number of eggs and egg rudiments produced in the ovaries, irrespective of whether or not they are subsequently laid.

(*b*) In the experiments set out in the warehouse, technique was slightly different. The moths were caught in the light and in the dark parts of the warehouse, sexed and placed singly in 3-inch by 1-inch tubes. All the tubes contained a small amount of grain to control the relative humidity and to provide an oviposition site for the females. The tubes were examined twice a week, when the females were transferred to clean tubes with fresh grain. All the used tubes were taken back to the laboratory and the number of eggs laid was counted. Only the fertilised females were used, and the eggs laid by the "calling" females (which were probably unfertilised) were not included in the total count. As the ages of the moths were not known, it was assumed that the large number used (526 females, 370 males) contained moths of all ages. It was assumed that the moths had lived half their life before capture and laid half their number of eggs.

The statistical methods used were derived from: (*a*) R. A. Fisher, *Statistical Methods for Research Workers*, Edinburgh, 1928; (*b*) K. Mather, *Statistical Analysis in Biology*, London, 1943.

B. Longevity and fecundity of the wild stock reared on Manitoba Wheat (*See* Table 1).

1. In 1943 method (*b*) was used in estimating the fecundity and longevity of the warehouse moths. The average fecundity of the 526 females of the first generation was 124 eggs (with the maximum of 213) and the average longevity of the females was 23·4 days and of the males 19·9 days, at the average temperature of 16·2° C., 62·9 per cent. R.H. The average fecundity of the 63 second generation moths was

79 eggs (100 maximum) with longevity of the females 73 and of the males 25 days, at the average temperature of 13·2° C., 63·9 per cent. R.H.

2. In 1944 a more direct method was used. 1943 warehouse larvae reared on Manitoba wheat were brought to Slough and allowed to diapause through the winter in a unheated outhouse. These larvae were divided into three groups. (i) Group 1 was kept in outdoor conditions throughout the period of pupation, pairing and oviposition. (ii) Group 2 was brought into 25° C. 70 per cent. R.H. at the time of pupation, and the emerged and paired moths were allowed water to drink. (iii) Group 3 was also kept at 25° C., 70 per cent. R.H., from the time of pupation. These moths were not given water to drink.

Only Group 1 moths were weighed on emergence. Post-mortem dissections were made of the moths of the three groups.

3. In 1945 all the moths were weighed on emergence, and although the treatment was the same as in 1944, none of the moths had access to water.

The results of these experiments are summarised in Table 1 and discussed below.

(i) *Relation between the weights of the moths on emergence with fecundity and longevity.*

Great variations in the total egg numbers were encountered, even when the females were reared under apparently comparable conditions. When the moths were weighed on emergence, clear correlations emerged between their weights and the fecundity of the females and longevity in both sexes. Thus in 1944 the average weight of 33 females was 7·8 mg. (4·0 mg. min., 11·0 mg. max.), the average egg number per female was 79 (10 min. and 169 max.), and the average length of life 12·5 days (5 min. and 32 max.). The average egg number per female below 8 mg. in weight was 57, the average longevity being 8·6 days, whereas the average fecundity of the females above 9·0 mg. in weight was 103 eggs and the longevity 16·6 days.

The regression coefficient of fecundity on weight of females at emergence was significant ($p < \cdot 001$). The regression coefficient of longevity on weight of females at emergence was also significant ($p < \cdot 001$) (fig. 1). The correlation coefficient between the longevity of 29 males and their weight on emergence was significant ($r = +0{\cdot}5189$, $n = 27$), as was the regression coefficient.

There was a significant correlation coefficient between the weights and fecundity of the females which had emerged in the warehouse. This observation was made by collecting pairing moths, weighing the females and considering the fecundity of those which, on dissection after death, contained one spermatophore only—*i.e.*, newly emerged females which could not have laid eggs before they were collected. The number of these moths in 1944 was 14, their average weight 10·0 mg. (6·0 mg. min., 12·0 mg. max.). The number of eggs laid by each one of them varied between 57–181, while the average was 104, and the

TABLE 1.—Average fecundity and

Date	Treatment	Average Temperature and percentage R.H.	Number of Moths	Average Fecundity	Max. Egg number
vi.–viii. (1943) First generation	Method (*b*) Moths kept in warehouse. —Water to drink.	16·2° C. 62·9 per cent. R.H.	♀ 526 ♂ 370	124	213
viii.–x. (1943) Second generation.	Method (*b*) Moths kept in warehouse. —Water to drink.	13·2° C. 63·9 per cent. R.H.	♀ 63 ♂ 66	79	100
vi.–vii. (1943)	Method (*a*) +Water to drink.	25° C. 70 per cent. R.H.	♀ 22	115	242
vi.–vii. (1944)	Method (*a*) Moths kept in unheated outhouse. —Water to drink.	16·2° C. 68·5 per cent. R.H.	♀ 33 ♂ 29	79	169
vi. (1944)	Method (*a*) —Water to drink.	25° C. 70 per cent. R.H.	♀ 24 ♂ 24	105	146
vi.–vii. (1944)	Method (*a*) +Water to drink.	25° C 70 per cent. R.H.	♀ 18 ♂ 14	108	195
vi.–vii. (1945)	Method (*a*) Moths kept in unheated outhouse. —Water to drink.	17·75° C. 79·8 per cent. R.H.	♀ 22 ♂ 19	67	104
vi.–vii. (1945)	Method (*a*) —Water to drink.	25° C. 70 per cent. R.H.	♀ 17 ♂ 15	82	214

longevity of moths bred on Manitoba wheat.

Percentage Hatch	Period of Incubation (days)	Pre-oviposition Period (days)	Average Longevity (days)	Average Weight (mg.)	Additional Notes
—	—	—	♀ 23·4 ♂ 19·9	—	—
—	—	—	♀ 37 ♂ 25	—	—
78·4	6·0	0·5	—	—	—
89·3	11·8	1·9	♀ 12·5	♀ 7·8 ♂ 6·6	Regression of fecundity on weight in ♀: $b=13{\cdot}675$, $t=5{\cdot}397$, $p<{\cdot}001$. Regression of longevity on weight in (*a*) ♀: $b=1{\cdot}872$, $t=5{\cdot}589$, $p<{\cdot}001$. (*b*) ♂: $b=1{\cdot}333$, $t=3{\cdot}154$, $p<{\cdot}01$.
83·4	5·6	0·6	♀ 6·5 ♂ 8·2	—	Average number of egg rudiments of newly emerged ♀=206. Number of eggs laid=105. Number of rudiments remaining after death=102. (105+102=207.)
82·7	5·6	0·4	♀ 9 ♂ 8	—	
—	—	2·0	♀ 9·7 ♂ 8·2	♀ 6·7 ♂ 5·4	Regression of fecundity on weight in ♀: $b=12{\cdot}080$, $t=4{\cdot}472$, $p<{\cdot}001$. Regression of longevity on weight in (*a*) ♀: $b=1{\cdot}722$, $t=7{\cdot}059$, $p<{\cdot}001$; (*b*) ♂: $b=1{\cdot}675$, $t=6{\cdot}322$, $p<{\cdot}001$.
—	—	0·8	♀ 6·6 ♂ 6·5	♀ 6·7 ♂ 5·5	Regression of fecundity on weight in ♀: $b=21{\cdot}992$, $t=10{\cdot}404$, $p<{\cdot}001$. Regression of longevity on weight in (*a*) ♀: $b=0{\cdot}851$, $t=5{\cdot}236$, $p<{\cdot}001$. (*b*) ♂: $b=0{\cdot}77$, $t=1{\cdot}695$, $p<{\cdot}2$.

correlation coefficient between the initial weights of the females and fecundity was again significant ($r = +0{\cdot}6252$ $p = > {\cdot}01$ $< {\cdot}02$).

Similar relationship between the initial weights of the once paired warehouse moths and fecundity was obtained in 1945 and is given in Table 2. These moths were collected at the beginning of the maximum emergence period (28.vi.45), hence it was possible to obtain the large

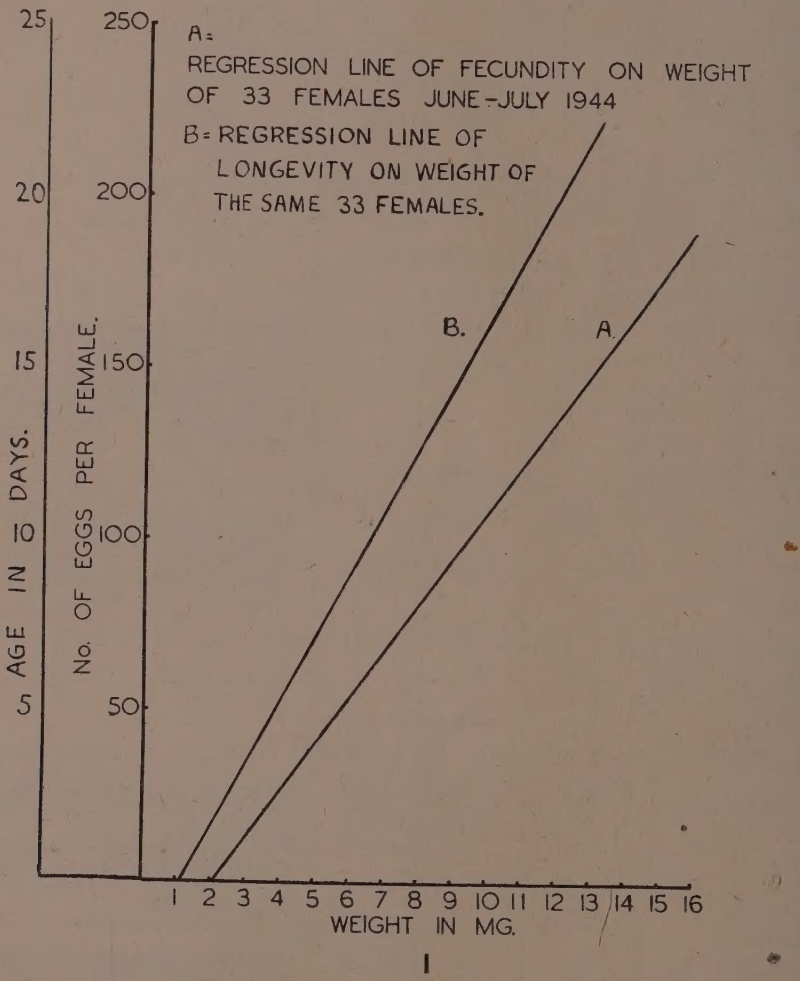


FIG. 1.—Regression line of fecundity on weight in 33 females kept at outdoor temperatures, June–July, 1944. The value of *b* (*i.e.*, increase in egg number per mg. weight of moth) was 13·675.

Regression line of longevity on weight in 33 females kept at outdoor temperatures, June–July, 1944. The value of *b* (*i.e.*, increase in longevity in days per mg. weight of moth) was 1·872.

number of newly emerged females on one day. Again, in the laboratory experiments in 1945 the regression coefficients relating fecundity to weights of moths and fecundity were significant, both at fluctuating outdoor temperatures and at 25° C., 70 per cent. R.H. (see Table 1).

TABLE 2.

Relationship between the initial weights of the warehouse females and fecundity.

Initial weight of females (mg.)	1·5	3	4	4·5	5	5·5	6	6·5	7	7·5	8	8·5	9	9·5	10	10·5	11·5
Number of eggs laid by a female	0	21	0 46 32	98 0	53 57 42	54 78	43 70 100 59 56	72 76 79 82	72 60 81 110 92 75	73 99	95 118 61 91 94 112 73	115	128 86	142 101	138 125 126	105	117
Number of moths (Total=46)	1	1	3	2	3	2	5	4	6	2	7	1	2	2	3	1	1
Number of eggs per female	0	21	26	49	51	61	66	77	82	86	92	115	107	122	126	105	117

The relation of longevity and the initial weights in both sexes, at fluctuating outdoor temperatures, were also significant, but whereas p was $<\cdot001$ for the females at 25° C., 70 per cent. R.H., no significant relationship appeared in the males at this temperature.

(ii) *The effect of temperature on fecundity and longevity of the moths.*

It can be seen from Table 1 that the fecundity of the moths increases, while longevity decreases, with the rise in temperature. The average number of eggs laid by the first generation of moths in 1943 was 124 at the average temperature of 16·2° C., 62·9 per cent. R.H. The corresponding figure for the second generation was 79 at the average temperature of 13·2° C., 63·9 per cent. R.H. In comparable sets of experiments in 1944 and 1945, higher average egg numbers were laid by the moths at 25° C., 70 per cent. R.H., than at the lower, fluctuating temperatures. Thus in 1944 the average fecundity of 33 females averaging 7·8 mg. in weight was 79 at fluctuating temperatures, while that of 24 females kept as pupae and moths at 25° C., 70 per cent. R.H., was 105. It is interesting to note that the average number of ovarial rudiments and ripe eggs in 22 newly emerged females (of average weight 6·5 mg.) kept as pupae at 25° C., 70 per cent. R.H., was 206. As has been said, the number of eggs laid by these females was 105, while the average number of rudiments remaining in the ovaries at death was 102. This gives the total of 207, which coincides with the average of 206 of the newly emerged females, and strongly suggests that all, or nearly all, the egg rudiments are already present in the ovaries at the time of emergence. Sixty-five per cent. of these females died with their fat bodies exhausted, and since the food reserve in the fat body was used up, it seems probable that no more eggs could have been ripened in these individuals. However, the close coincidence of these figures is only an approximation, as

a subsequent experiment suggested that a certain number of egg rudiments are resorbed by the fertilised females. In this experiment the pupae were kept at 25° C., 70 per cent. R.H., till emergence. One half were dissected on emergence and the other half kept for egg laying and dissected after death. There were 28 moths in each group and the average weight of both groups was 6·98 mg. (*i.e.*, the moths were strictly comparable).

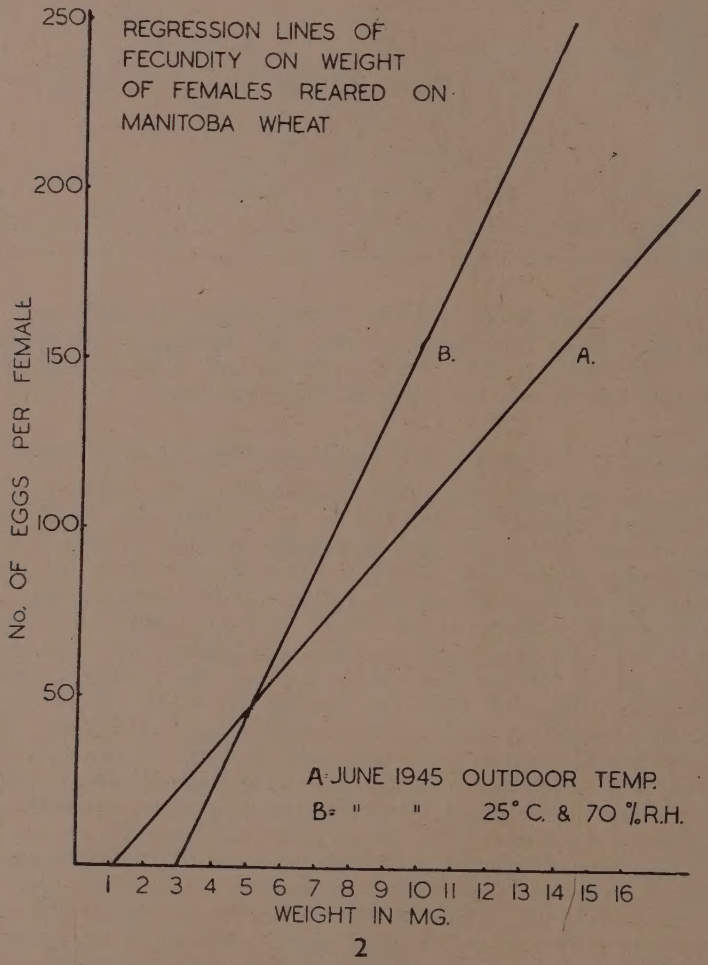

REGRESSION LINES OF FECUNDITY ON WEIGHT OF FEMALES REARED ON MANITOBA WHEAT
No. OF EGGS PER FEMALE
250
200
150
100
50
B.
A.
A-JUNE 1945 OUTDOOR TEMP.
B- " " 25° C. & 70 % R.H.
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
WEIGHT IN MG.
2

FIG. 2.—Regression lines of fecundity on weight of females reared on Manitoba wheat. The value of *b* (*i.e.*, increase in fecundity per mg. weight of moth) at outdoor temperatures was 12·08; at 25° C., 70 per cent. R.H. it was 21·992. These results differ significantly ($p < ·01$).

The result was as follows :—

Average number of rudiments at emergence (potential fecundity) 259
Average number of eggs laid (actual fecundity) 91
Average number of eggs laid plus rudiments remaining after death 214

The average resorption, or loss of rudiments, by the fertilised females was therefore 17 per cent.

The effect of different temperatures during the pupal period on the number of rudiments at emergence was also tested. Larvae from out-door temperatures were put at 25° C., 70 per cent. R.H., in March. After pupation these were divided into two groups, one kept at 25° C., and the other put back into out-door temperatures. The ones at 25° C. emerged six weeks earlier than those in fluctuating conditions. The moths were dissected on emergence and the rudiments counted. The result was as follows :—

23 moths at 25° C. (average weight 7·4 mg.)—average number of rudiments 264
23 moths at outdoor temperatures (average weight 7·3 mg.)—average number of rudiments 237

The difference in number of egg rudiments between the two groups was not significant, suggesting that temperature during the pupal period alone has no very marked effect on the number of rudiments.

TABLE 3.

Regression coefficients of fecundity and longevity on weights at emergence of moths emerging June, 1945.

Temperature	No. moth n	Average weight (mg.) $\bar{x}$	Average fecundity $\bar{y}$	Average longevity $\bar{y}$	Slope of line b	t	p
25° C., 70 per cent. R.H.	17 ♀	6·7	82·6	—	21·992	10·404	<·001
	,,	,,	—	6·6	0·851	5·236	<·001
	15 ♂	5·5	—	6·5	0·77	1·695	<·2
Outdoor (Fluctuating)	22 ♀	6·7	67	—	12·080	4·472	<·001
	,,	,,	—	9·7	1·722	7·659	<·001
	23 ♂	5·4	—	8·2	1·675	6·322	<·001

In 1945 the weights of the female moths at fluctuating outdoor temperatures and at 25° C., 70 per cent. R.H., averaged 6·7 mg. in both sets. The regression coefficients of fecundity on weight, and longevity on weight, were significant in each set (Table 3 and fig. 2). Comparing the sets by the formula $t = V\dfrac{b_1 - b}{\overline{Vb_1} + \overline{Vb_2}}$, coefficients relating fecundities to weights were significantly different at the two temperatures—*i.e.*, p was <·01. From the values of b it was possible to assess the increase of 12 eggs per mg. of weight at fluctuating temperatures, as compared with the corresponding increase of 21 eggs at 25° C., 70 per cent. R.H.

The variance of longevity at the two sets of temperatures was great, and no significant results were obtained. It is difficult to assess the effect of rise of temperature independently of the other factors, but it would seem that at least two opposing processes are operating: (1) fecundity tends to be greater at higher temperatures, (2) on the whole, longevity decreases with the rise in temperature, probably as a result of greater metabolic rate. This has been noted by a number of authors, among them by Norris (1933) in *Ephestia kuhniella* L. and by Eastham and McCully (1943) in *Calandra granaria*.

The effect of temperature on the life history as a whole, and on the resulting fecundity, is even more complicated. When single larvae were reared on a sufficient quantity of Manitoba wheat, heavier moths emerged at 17° C. and 21° C. than at 25° C., 70 per cent. R.H. The weights of these moths are given in Table 4.

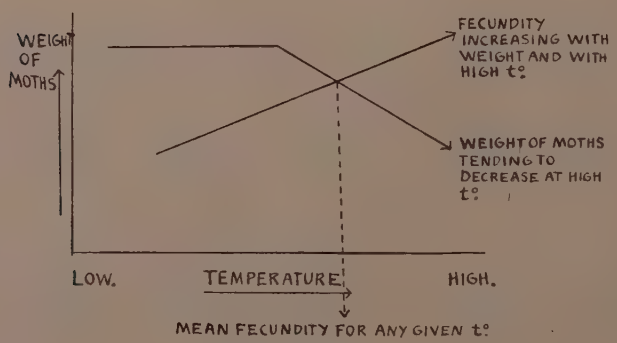
TABLE 4.

Weights of moths reared singly as larvae on Manitoba wheat, at different temperatures and 70 per cent. R.H.

	17° C.	21° C.	25° C.
No. of ♀ moths ...	22	31	30
Average weight (mg.)	10·1	10·6	9·7
No. of ♂ moths ...	22	33	32
Average weight (mg.)	8·1	8·9	7·7

As fecundity is directly affected by increase in weight, which occurs at lower temperatures, and at the same time decreases with the fall in temperature, two opposing processes must be operating, and it would seem that at least at constant temperatures there must be limits within which the maximum ripening of the eggs may be expected.

EFFECT OF TEMPERATURE ON THE LIFE HISTORY AS A WHOLE AND THE RESULTING FECUNDITY.


WEIGHT OF MOTHS
FECUNDITY INCREASING WITH WEIGHT AND WITH HIGH t°
WEIGHT OF MOTHS TENDING TO DECREASE AT HIGH t°
LOW.
TEMPERATURE
HIGH.
MEAN FECUNDITY FOR ANY GIVEN t°

These two processes may be represented graphically as follows (fig. 3) :—

The low numbers of eggs laid by the moths at lower temperatures cannot be explained by the decrease in potential fecundity—*i.e.*, by the decrease in the number of ovarial rudiments. Thus in 1944 the average number of egg rudiments in 23 virgin females of the second autumn generation moths was 298 (with the maximum of 448) as compared with the average[2] of 258 (maximum 384) of the 21 summer generation moths. The lower egg output must be due to the direct inactivating effect of the lower temperatures, and the inability of the moths to pair below a certain minimum temperature. This inactivity can be assessed by the numbers of spermatophores in the bursa copulatrix of the females, since each one represents one pairing. This number averaged 3·1 in the females with exhausted fat bodies (*i.e.*, those which had laid the full number of eggs) throughout the first generation. The greatest number of spermatophores found was 7, and several moths had 6 or 5. In the second generation there were many virgin females, and many which had only paired once.

A suggestion that the decrease in fecundity of the second generation moths is also due to partial sterility of the males at low temperatures was obtained from the following observations, which are, however, of a preliminary nature.

Twenty-nine moths collected in the unheated granary in November were brought back to the laboratory.

(*a*) Ten females were dissected ; of these 3 were virgin and 7 fertilised ; 4 of the fertilised females had numerous egg rudiments.

(*b*) Seven other females were placed at 25° C., 70 per cent. R.H. Dissections after death showed that 3 of the 7 were virgin, and the 4 fertilised females laid only 4 eggs on the average, although the ovaries again contained numerous egg rudiments. Thus high temperature did not increase the number of eggs laid.

(*c*) Seven of the laboratory stock males were crossed with 7 warehouse females at 25° C., 70 per cent. R.H. Dissections after death showed that 2 females remained virgin, while the average fecundity of the 5 others was 79.

(*d*) Five of the second generation warehouse males were crossed with the laboratory stock females. Two of these females remained virgin, while the average egg output of the 3 others was only 19 eggs.

The direct effect of the rise and fall of temperature on the length of the preoviposition period and the egg incubation period is very clear (see Table 1). Eggs kept in the laboratory at 17° C., 21° C., 25° C., 70 per cent. R.H., took 13–15, 9–10 and 4–6 days respectively to hatch.

---

[2] On comparing the two means by the "t" test p was $>\cdot01<\cdot02$.

(iii) *Effect of giving moths water to drink on fecundity and longevity.*

Some of the results of these experiments are summarised in Tables 1 and 6. Twenty-three of the females kept at 25° C., 70 per cent. R.H., without access to water, were dissected after death. The results were as follows :—

Average number of eggs laid		106
Average number of egg rudiments remaining in ovaries ...		102
Average longevity	days	6·8
Percentage with exhausted fat bodies		65

Similar post-mortem dissections of 20 females paired and kept at 25° C., 70 per cent. R.H., but given water to drink, gave the following results :—

Average number of eggs laid		103
Average number of egg rudiments remaining in the ovaries ...		81
Average longevity	days	9·4
Percentage with exhausted fat bodies		89

Since the average number of eggs laid by these moths was very similar to that laid by non-drinkers, the giving of water would seem to have no effect in this particular set of moths. At the same time not only was the average number of rudiments remaining in the ovaries smaller in the drinkers, but the ovaries had quite definitely a more exhausted and shrunken appearance. When increased longevity and the greater percentage of moths with exhausted fat bodies are also taken into consideration, it seems probable that fecundity may be slightly increased by water drinking. Moreover, 94 per cent. of the 17 males which had access to water died with exhausted fat bodies, as compared with 85 per cent. in the 26 non-drinkers. As these moths were not weighed, it is conceivable that smaller moths were used in the second experiment. On the other hand, the effect of drinking water on the fecundity of the laboratory stock was very marked : 30 per cent. and 37 per cent. more eggs were laid by the moths bred on middlings and on Manitoba wheat respectively when the females had access to water. Norris (1934) found that the fecundity of *E. elutella* moths given water to drink was nearly 50 per cent. greater than of those given no water. It would appear, therefore, that the reactions of all stocks to this factor are not the same.

(iv) *Longevity of virgin females and resorption of egg rudiments.*

Virgin females live longer than the fertilised females. In one experiment with moths reared on Manitoba wheat and kept at 25° C., 70 per cent. R.H., the average longevity of fertilised females was 10 days, while that of virgin females was 13·5. Similarly the average total life of 4 fertilised females reared on "middlings" and kept at 25° C. was 9·3 days, and that of 14 virgins was 15·9. It is possible that the longer life of the virgin females is not only due to the lesser activity, but also

to resorption of the eggs. These females usually lay a small number of eggs, none of which have been observed to hatch. When 14 laboratory stock virgin females of 6·2 mg. average weight were dissected, the average number of egg rudiments was found to be 245. Another 14 females of 6·2 mg. average weight from the same source were kept virgin at 25° C., 70 per cent. R.H. When the number of eggs laid by these females is added to the rudiments left in the ovaries an average of only 148 is obtained. This diverges from the expected 245 and indicates that resorption of about 40 per cent. of the eggs occurred throughout the lifetime. It has already been pointed out in Section B (ii) that only 17 per cent. of the rudiments were resorbed in fertilised females.

C. The effect of diapause and utilisation of the stored food materials in the larvae on the fecundity of the moths.

In outdoor conditions only a small number of the larvae pupate and emerge as the second generation. The majority of the larvae spin up and go into diapause for 9–10 months. If these larvae are placed at 25° C. at the beginning of diapause (September–November) only a few will pupate, if they are placed at 25° C. in January and later, they all pupate within a fortnight (average time 13·6 days). During the period of quiescence the larvae show progressive loss in weight, and progressive loss in the total fat content (from 47·5 per cent. of dry weight in November to 40·8 per cent. in May (Waloff, *in preparation*). As the fat body is said to be a store not only of fats but also of proteins (Wigglesworth, 1939), the reduction in the fat content is probably no more than an index of a more generalised utilisation of the reserve food materials, especially as elimination of nitrogenous waste products, through the malpighian tubes, is continuous throughout the period of quiescence.

In 1944 diapausing larvae were placed at 25° C. in February. The moths which emerged from them were paired, but unfortunately they were not weighed. The average fecundity of 10 females kept at 25° C. and given access to water was 132 (minimum 80, maximum 192). The

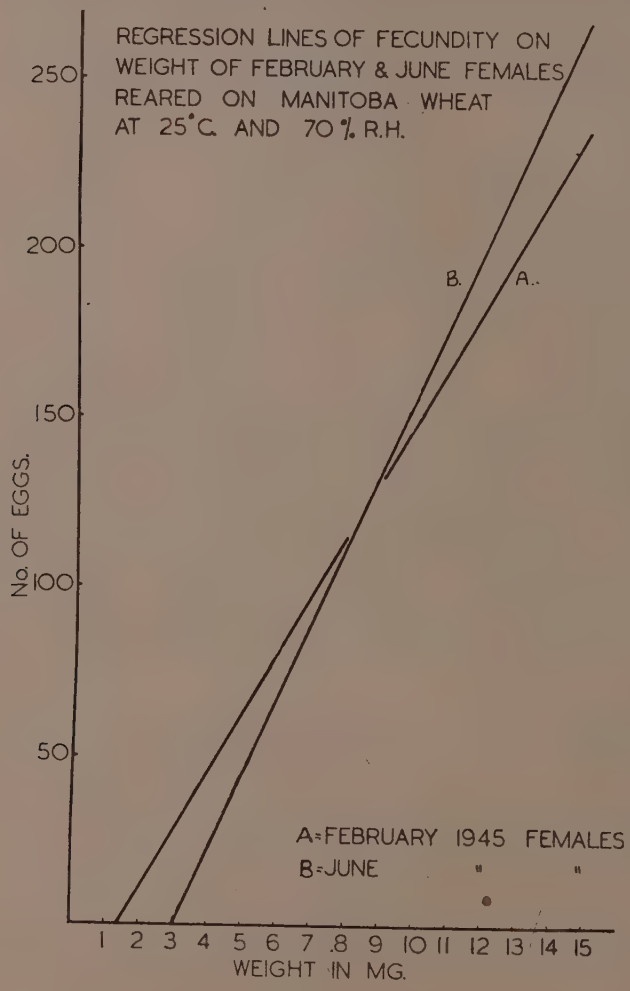
TABLE 5.

Average weights, fecundity and longevity of moths from the same larval stock, pupating at 25° C. in February and at the normal time of emergence—June.

Date	Treatment	No. of moths	Average weight of moths (mg.)	Average fecundity	Maximum egg No.	Average longevity (days)
ii.–iii.1945	Diapausing larvae from outdoor temperatures placed at 25° C. on 30.i.45. Emerged ii.–iii.45	♀ 21 ♂ 20	♀ 7·5 ♂ 5·6	105	193	♀ 8·9 ♂ 8·5
vi.–vii.1945	Diapausing larvae from outdoor temperatures placed at 25° C. at the normal time of pupation.	♀ 17 ♂ 15	♀ 6·7 ♂ 5·5	82	214	♀ 6·5 ♂ 5·5

average fecundity of 18 drinkers at 25° C., 70 per cent. R.H., emerging in June–July (*i.e.*, at the normal time) was 108 (minimum 36, maximum 195). This experiment was repeated in 1945, when all the moths were weighed, and the results are set out in Table 5.

The weight of the female moths emerging in February was 7·5 mg. and that of those emerging in June was 6·7 mg. The corresponding average fecundities were 105 and 82 eggs per female. The regression



4

FIG. 4.—Regression lines of fecundity on weight of females emerging in February and in June at 25° C., 70 per cent. R.H. In the first case the value of *b* (*i.e.*, increase in fecundity per mg. of moth weight) was 17·175, in the second 21·992. These values are not significantly different.

coefficients of fecundity on weights were very significant in both sets; in February moths, b was 17·175, t was 5·631 and $p<·001$; in June moths, b was 21·992, $t=10·404$ and $p<·001$. Similarly the regression coefficients relating longevity to weights of the February and June female moths were highly significant: in the February moths, b was 0·1372, $t=4·473$, $p<·001$, and in June moths b was 0·851, $t=5·236$, and $p<·001$. The regression coefficients of longevity on weight of male moths were as follows: in February males, b was 0·670, $t=7·335$, $p<·001$, while in June males b was 0·77, $t=1·695$, $p<·2$ (not signif.). The regression coefficients of fecundity on weight of the February and June moths did not differ significantly, indicating that the actual difference was due to the heavier weight of the early moths, and that the females of the same weights would tend to have the same fecundities at different times of the year (fig. 4).

"t" tests applied to the longevities of the February and June moths were significant, and for both females and males p was $<0·01$.

This significant difference in longevities, together with the greater weight of the early female moths (and associated greater fecundity), may be the result of the shortened period of quiescence, and hence of the lesser degree of utilisation of the larval reserve materials.

A similar result was obtained from the counts of the numbers of ovarial rudiments in the first (*i.e.*, diapausing) and in the second generation of moths, which arises from non-diapausing larvae in the granary. The average number of egg rudiments, including ripe eggs, in the virgin females of the first generation was 258, with the maximum of 384, and that of the second generation virgins 298, with the maximum of 448. This higher number of egg rudiments may also be associated with the lesser utilisation of reserve food in the non-diapausing larvae.

D. The effect of larval food on the fertility and fecundity of the adults.

(i) *Preliminary experiments with a non-diapausing stock of larvae.*

These were the initial experiments of this series, and the moths were from the laboratory stock. This stock is derived from non-diapausing larvae which have been isolated in the Slough laboratory (E. Basden, *unpublished*), and produces continuous generations throughout the year at 24–25° C., 70 per cent. R.H. Considerable difficulties were met in handling these moths, as it was found that this stock pairs less readily than the wild one, and the number of fertilised females is low, as is the number of larvae hatching from the eggs. Except at low outdoor temperatures in autumn, almost all the warehouse females paired readily when put with males, whereas the percentage of paired females in the laboratory stock ranged between 31·5 and 73·3. For a series of years this stock has been reared at 24° C., 70 per cent. R.H., and it is possible that this constant and high temperature has affected the fertility of the moths. This is substantiated by the fact that when Norris (1934) worked with these moths she did not encounter similar difficulties and obtained the mean fecundity of 298 eggs when the moths had access to water,

and 159 in the non-drinkers. During the present experiments the mean fecundity did not exceed 128, although the egg rudiment number was very high. It is known that the temperature of 27° C. effects spermatogenesis in *E. kuhniella* (Raichoudhury, 1936; Norris, 1933), and it is not impossible that the temperature of 24°–25° C. at which *E. elutella* is reared is too high for the normal development of this moth, which is said to be indigenous to a more temperate climate. Large numbers of *E. elutella* are found in the unheated warehouses in this country, whereas *E. kuhniella* occurs in large numbers only in heated mills. Moreover, *E. elutella* has been reported from outdoor haystacks in Central Europe (Richards and Thomson, 1932). The experiments with the laboratory moths are summarised in Table 6.

TABLE 6.

Fecundity of laboratory stock ♀ at 25° C, 70% R.H.

Larval Food	Water to drink	Number of Females		Longevity of Females (days)			Average Fecundity	Max. number of eggs	Percentage Hatch	Incubation Period (days)
		Total	Fertilised	Fertilised		Unfertilised				
				Preoviposition	Total					
Middlings	—	11	4	0	9·3	15·9	71	121	55·6	6·3
Middlings	+	11	4	0·25	12	7·3	92	161	74·4	5·8
Glycerine and Wheatfeed	+	30	22	0·25	12	13·5	128	178	67·8	4·5
Manitoba Wheat	—	19	6	0·66	10	13·5	70	130	61·1	6·5
Manitoba Wheat	+	16	12	0·58	7·6	Not kept	96	146	Not kept	—

Although the numbers of fertilised females were low, two results became apparent. There was no obvious difference in the fecundity of the moths reared as larvae on middlings or on Manitoba wheat. In both sets of moths fecundity increased when the females had access to water—by 30 per cent. in the moths reared on middlings, and by 37 per cent. in those reared on wheat. It has been found (E. Basden, *unpublished*) that the addition of glycerine to the larval diet of middlings or wheat-feed considerably increases the egg output of *E. elutella*. The highest average fecundity in this set of experiments (128 eggs per female) was encountered in the moths reared as larvae on this diet. As glycerine readily absorbs water, it is possible that the high water content of the larval food affected the fecundity of the adults.

The effect of addition of glycerine to the larval food on the fat body of the adults has not been investigated.

(ii) *Experiments with the diapausing stock of larvae.*

These experiments were much more extensive, and the numbers of egg rudiments in the newly emerged females were primarily considered.

Fourteen two-pound jam-jars were set up containing 100 gms. of the following foods :—

2 Maize (coarse ground).
2 Manitoba wheat (coarse ground).
2 Sultanas.
2 Middlings (Toppings).
2 Soya grits.
2 Peanuts (coarse ground).
2 Cacao (coarse ground).

The jars were divided into two sets, A and B. In jars of series A were put 130 larvae derived from many pairs of warehouse moths. These hatched between 28.vi. and 22.vii.1944. In jars of series B were put 80 larvae from the same source, hatching between 25 and 28.vii.1944. All were reared in an unheated incubator in an outhouse, and emerged as moths the following summer.

On emergence all the females were weighed and dissected for the number of egg rudiments, except in the case of some of those reared on wheat and maize. Some of the females from these two foods were paired and kept for oviposition at room temperatures. They were given drinks of water on blotting paper every few days.

The data from these experiments are summarised in the following Tables 7 and 8 and in fig. 5.

TABLE 7.

Number of egg rudiments and weights (mg.) of females from diapausing larvae reared on different foods.

Food	Maize	Wheat	Sultanas	Middlings	Soya	Peanuts	Cacao
Emerged ♂	46	31	6	43	31	10	17
Emerged ♀	54	29	8	26	32	11	19
Total	100	60	14	69	63	21	36
Date first moth emerged	12.vi.45	18.vi.45	18.vi.45	6.vi.45	12.vi.45	18.vi.45	18.vi.45
Average weight, ♀ (mg.)	10·0	7·0	6·3	7·0	8·9	10·1	7·2
Average number of rudiments	359	259	213	262	293	345	244
Number of moths dissected	45	30	8	26	26	8	15

Regression coefficients of the numbers of egg rudiments on weight were worked out for each food and compared. None of them differed significantly and b fell between 17·7 and 28·05. The value of b for each food was as follows :—

Food	b
Middlings	24·9
Soya grits	28·05
Wheat	22·03
Sultanas	25·5
Cacao	17·7
Peanuts	26·7
Maize	25·8
Average	24·4

TABLE 8.

Fecundity of moths from diapausing larvae reared on maize and wheat.

Food	No., females	Average weight (mg.)	Fecundity			Longevity (days)	Condition after death	
			Average	Max.	Min.		Ovary	Fat body
Maize	14	11·2	179	327	93	13·1	Exhausted in 11/13	10/13
Wheat	15	7·0	74	145	33	8·7	Exhausted in 14/15	10/15

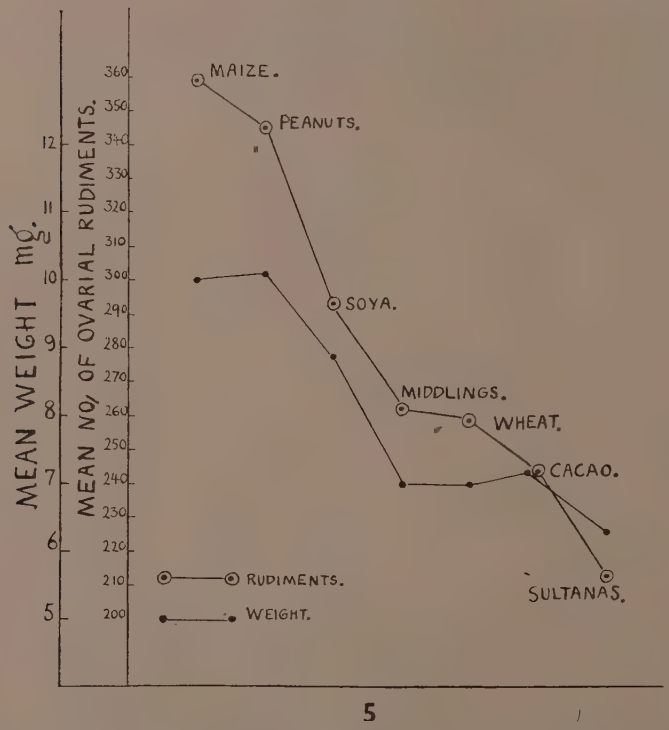


FIG. 5.—The mean number of egg rudiments and mean weights of moths reared on different foods.

In other words, the nature of the larval food increases the average number of egg rudiments only through its effect on the weight of the larva, there being no selective effect on egg production. There is roughly an increase of 24 rudiments for every gram of weight.

The weights of the moths appear to be directly dependent on the nature of larval food, and the following table (9) indicates all cases where their means differed significantly.

TABLE 9.

Significance of difference of means of weights (mg.) of moths reared on different foods.

	Middlings	Soya	Maize	Wheat	Sultanas	Peanuts
Soya	$p<\cdot01$					
Maize	$p<\cdot001$	$p<\cdot001$				
Wheat		$p<\cdot01$	$p<\cdot001$			
Sultanas		$p<\cdot01$	$p<\cdot001$			
Peanuts	$p<\cdot01$			$p<\cdot01$	$p<\cdot001$	
Cacao		$p=\cdot01$	$p<\cdot001$			$p<\cdot01$

As to fecundity, those fed on maize laid more eggs than those on wheat, the difference being almost the same as that between the rudiments of the two groups. The maximum number of eggs laid by the maize-fed moths was 327 and 6 moths (out of the total of 14) laid over 200 eggs. Their average longevities were also different—8·7 days for moths reared on wheat and 13·1 days for those reared on maize.

The moths fed on peanuts had nearly as high a rudiment number as those on maize, but the number of individuals emerging was very small and it was thus impossible to estimate their fecundity.

E. Oviposition.

As can be seen in fig. 6, most of the eggs are laid in the first three to four days after pairing. The preoviposition period varies in individual moths, and at different temperatures (Table 1), but most of the females start laying within the first twenty-four hours after pairing.

The length of the whole oviposition period extends for several days, tending to increase with the drop in temperature. Dick (1937) has subdivided the oviposition cycles in Coleoptera into four distinct groups: (1) short-lived adults, which lay all their eggs within a few days; (2) adults which live a long time and produce eggs continuously; (3) species which during one season lay eggs in batches at fairly short intervals of time; (4) species which lay more or less continuously in two or more seasons, separated by a period during which oviposition ceases. If this classification can be extended to other insects, then *E. elutella* clearly falls into group (1).

Some aspects of the behaviour of the ovipositing moths have been discussed elsewhere (Waloff and Richards, 1946) and only the salient points are noted here. It was found that at outdoor temperatures, and at fluctuating low light intensities, most of the eggs are laid in the evening and at night time. Although the females will lay readily even

in empty glass tubes, they are strongly chemotactic and will lay eggs on grain in preference to other surfaces, such as sacking, brick or wood. They are even more strongly attracted to the smell of cacao beans, seemingly irrespective of whether they were reared on grain or on cacao as larvae.

There is little uniformity in the way the eggs are laid. They may be deposited singly, or in neat rows along crevices, such as grain grooves, or again they may be laid on top of one another in large bunches. It was noted that each female, generally, was consistent in the way she laid.

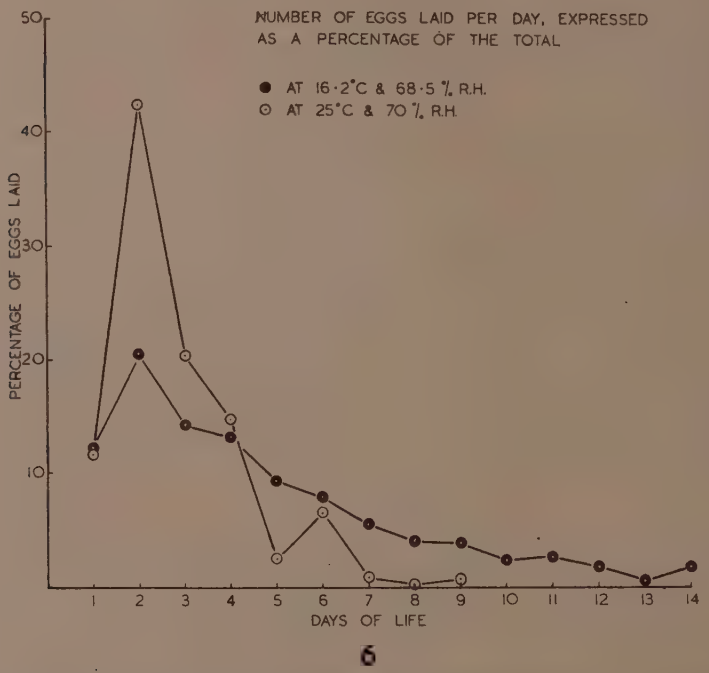

NUMBER OF EGGS LAID PER DAY, EXPRESSED AS A PERCENTAGE OF THE TOTAL
● AT 16·2°C & 68·5 % R.H.
⊙ AT 25°C & 70 % R.H.
PERCENTAGE OF EGGS LAID
50
40
30
20
10
1 2 3 4 5 6 7 8 9 10 11 12 13 14
DAYS OF LIFE
6

Fig. 6.—Number of eggs laid per day (expressed as percentage of the total) by females at outdoor temperatures and at 25° C., 70 per cent. R.H

F. Discussion.

The great divergence in the average fecundity of *E. elutella* quoted in literature is not surprising. Reed and Livingstone (1937), Bovingdon (1933), Belyaev *et al.* (1932) all quote instances of moths laying 200–300 eggs, but obtain much lower average numbers. None of these workers provided moths with water to drink.

It became clear from experiments on this species that not only the access to drinking water but the nature of larval diet affected both the actual and the potential fecundity of the moths. Thus, those reared on maize laid 179 eggs on the average (with the maximum of 327), whereas

a corresponding set reared on wheat had the mean fecundity of 74 with the maximum of 145. It was found that the actual and potential fecundity are both functions of the weight of moths on emergence, and that this weight is directly affected by the nature of the larval diet. Roughly, there is an increase of 24 rudiments per mg. of weight of the moths, independently of the food on which they have been reared—*i.e.*, a moth of x mg. reared on wheat will tend to have the same number of rudiments as a moth of x mg. reared on maize.

The problems of actual and potential fecundity are obviously very complex, and the factors affecting them are not necessarily the same. Some indications of this complexity have been obtained in these experiments, since actual fecundity depends not only on the initial weight of the moths and effect of drinking water, but also on the temperature at which these moths oviposit. There are also indications that the amount of the reserve substances in the larvae has a direct effect on the fecundity, as it affects the weights of adults. The moths which had a short period of larval diapause laid larger numbers of eggs than those which diapaused throughout the normal period of 9–10 months. Moreover, the number of egg rudiments in the virgins of the second, non-diapausing, wild generation was higher than that of the first annual generation derived from over-wintering larvae. When the effect of temperature on the whole life history and the subsequent fecundity is considered, the problem becomes even more complex, as the weights of the moths bear relation to the temperatures at which the larvae develop.

Some of these interactions may be summarised in the following way :—

Factors affecting fecundity of the adult females.

A. Indirect :
   1. Differences in larval nutrition.
   2. Temperatures at which the larvae develop even on the same food.
   3. Length of time the larvae diapause and utilise the reserve food materials.

B. Direct :
   1. Initial weights of adults (which may depend on A1, 2, or 3).
   2. Temperature at which eggs are laid.
   3. Access of moths to drinking water.

E. elutella is a warehouse pest, attacking foods as diverse as cacao, tobacco, dry fruit, oil seeds and grain, and, as the larvae may be introduced into new countries with these commodities, and the larval adult stages passed in widely different climatic conditions, the variabilities in fecundity encountered, and described in the literature, are hardly surprising. Moreover, isolation of certain strains may also occur in the established stocks.

The laboratory stock which has been selected for non-diapause at 24–25° C. is less fertile than the wild one. This decrease in fertility may be due to the direct, continuous effect of high temperature, or to certain lethal characters linked with non-diapause. It would be of great interest to know the effect of high temperature on the moths established in tropical countries, as the readiness with which this species enters diapause at low temperatures indicates that it is indigenous to a temperate climate.

G. Acknowledgements.

This work was done as a supplement to the study of a population of *Ephestia elutella* Hübner (Lep. Phycitidae) living on bulk grain, by O. W. Richards and N. Waloff (1946), in which detailed acknowledgements will be found.

H. Summary.

1. Longevity and fecundity of *E. elutella* reared on Manitoba wheat at 25° C., 70 per cent. R.H., and at outdoor temperatures were considered.

2. Fecundity and longevity of the females are the functions of their weight on emergence.

3. (*a*) Heavier moths emerged from larvae reared on Manitoba wheat at 17° C., 70 per cent. R.H., and 21° C., 70 per cent. R.H., than at 25° C., 70 per cent. R.H. This potentially increased their fecundity.

(*b*) Fecundity increases with temperature and simultaneously longevity decreases.

The effect of temperature on fecundity is thus twofold, and opposing processes are operating.

4. Temperature during the pupal period alone has no marked effect on the number of egg rudiments present in the newly emerged female.

5. The fecundity of the moths is slightly increased by providing them with drinking water.

6. Virgin females resorbed 40 per cent. and fertilised females 17 per cent. of their egg rudiments. The increased longevity of the virgins may be, at least partly, due to the greater resorption.

7. (*a*) Females with a shortened period of larval diapause (at 25° C., 70 per cent. R.H.) tend to be heavier than those emerging after the normal period of 9–10 months of quiescence. Correspondingly their fecundity is greater. It is suggested that this is due to the lesser utilisation of the larval reserve materials.

(*b*) Similarly, the number of ovarial rudiments in the newly emerged females of the second (non-diapausing) generation was greater than that of the first (diapausing) generation of moths.

The number of eggs actually laid by the second generation moths is, however, lower. This is probably due to the direct inactivating effect of low temperatures. It is also suggested that the males are more sterile at lower temperatures.

8. The weights of the moths and the number of their ovarial rudiments at emergence are proportional to and dependent on the larval diet. Roughly, there is an increase of 24 rudiments per mg. of weight of moth, irrespective of the larval diet. There is a corresponding increase in the number of eggs laid, and in longevity.

9. Most of the eggs are laid in the first 3–4 days after emergence; the females begin to lay within 24 hours after pairing.

10. The choice of oviposition sites is discussed.

References.

Belyaev, I. M., Schesterikova, M. N., Popov, P. V., 1932, Materials for the study of pests of stored oil seeds. *Schr. zent. biochem. Forsch. Inst. Nahr. Hund Genussmittelind.* **1** : 344–432. (In Russian with German summary.)

Bovingdon, H. H. S., 1933, Report on the infestation of cured tobacco in London by cacao moth *Ephestia elutella* Hb. *Rep. Emp. Mktg. Bd.* **67**.

Dick, J., 1937, Oviposition in certain Coleoptera. *Ann. appl. Biol.* **24** : 762–796.

Eastham, L. E. S., and McCully, S., 1943, The oviposition responses of *Calandra granaria* L. *J. exp. Biol.* **20** : 35–42.

Norris, M. J., 1933, Contributions towards the study of insect fertility : II. Experiments with factors influencing fertility in *Ephestia kuhniella* Z. (Lep. Phycitidae). *Proc. zool. Soc. Lond.* **1933** : 903–934.

——, 1934, Contributions towards the study of insect fertility : III. Adult nutrition, fecundity and longevity in the genus *Ephestia* (Lep. Phycitidae). *Proc. zool. Soc. Lond.* **1934** : 334–360.

Raichoudhury, D. P., 1936, Retardation of spermatogenesis and reduction of motility of sperm in *Ephestia kuhniella* Z. (Lep. Phycitidae) caused by high temperature. *Proc. zool. Soc. Lond.* **1936** : 789–805.

Reed, W. D., and Livingstone, E. M., 1937, Biology of the tobacco moth and its control in closed storage. *Circ. U.S. Dep. Agric.* **422**.

Richards, O. W., and Thomson, M. A., 1932, A contribution to the study of the genera *Ephestia* Gn. (including *Strymax*, Dyar.) and *Plodia* Gn. Lepidoptera, Phycitidae) with notes on parasites and larvae. *Trans. ent. Soc. Lond.* **80** : 169–250.

Richards, O. W., and Waloff, N., 1946, A study of a population of *Ephestia elutella* Hb. (Lep. Phycitidae) living on bulk grain. *Trans. R. ent. Soc. Lond.* **97** : 253–98.

Waloff, N., Some observations on the diapausing larvae of *Ephestia elutella* Hb. (Lep. Phycitidae) (*in preparation*).

Waloff, N., and Richards, O. W., 1946, Observations on the behaviour of *Ephestia elutella* Hb. (Lep. Phycitidae) breeding on bulk grain. *Trans. R. ent. Soc. Lond.* **97** : 299–335.

Wigglesworth, V. B., 1939, *The principles of Insect Physiology*. London.